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Plasticity of population coding in primary sensory cortex

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That experience shapes sensory tuning in primary sensory cortex is well understood. But effective neural population codes depend on more than just sensory tuning. Recent population imaging and recording studies have characterized population codes in sensory cortex, and tracked how they change with sensory manipulations and training on perceptual learning tasks. These studies confirm sensory tuning changes, but also reveal other features of plasticity, including sensory gain modulation, restructuring of firing correlations, and differential routing of information to output pathways. Unexpectedly strong day-to-day variation exists in single-neuron sensory tuning, which stabilizes during learning. These are novel dimensions of plasticity in sensory cortex, which refine population codes during learning, but whose mechanisms are unknown.

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Introduction

Sensory experience drives robust plasticity of sensory tuning and maps in sensory cortex. This well-studied process drives map development to match sensory statistics, and contributes to sensory perceptual learning [1–3]. But is there more to sensory cortex plasticity than changes in sensory tuning? Sensory areas use population codes that are based on coordinated spiking across many neurons. Large-scale population imaging and recording enable comprehensive analysis of population coding. Chronic longitudinal imaging allows plasticity to be directly observed, with cellular resolution, as it unfolds [4–6]. These methods provide new insight into neural coding and how it changes during plasticity. Recent studies confirm changes in sensory tuning, but also reveal plasticity in other aspects of population coding, including response gain and variability, firing correlations, and top-down modulation by task context. Here we review some key findings, which suggest novel sites and mechanisms for sensory cortex plasticity.

Plasticity of sensory tuning

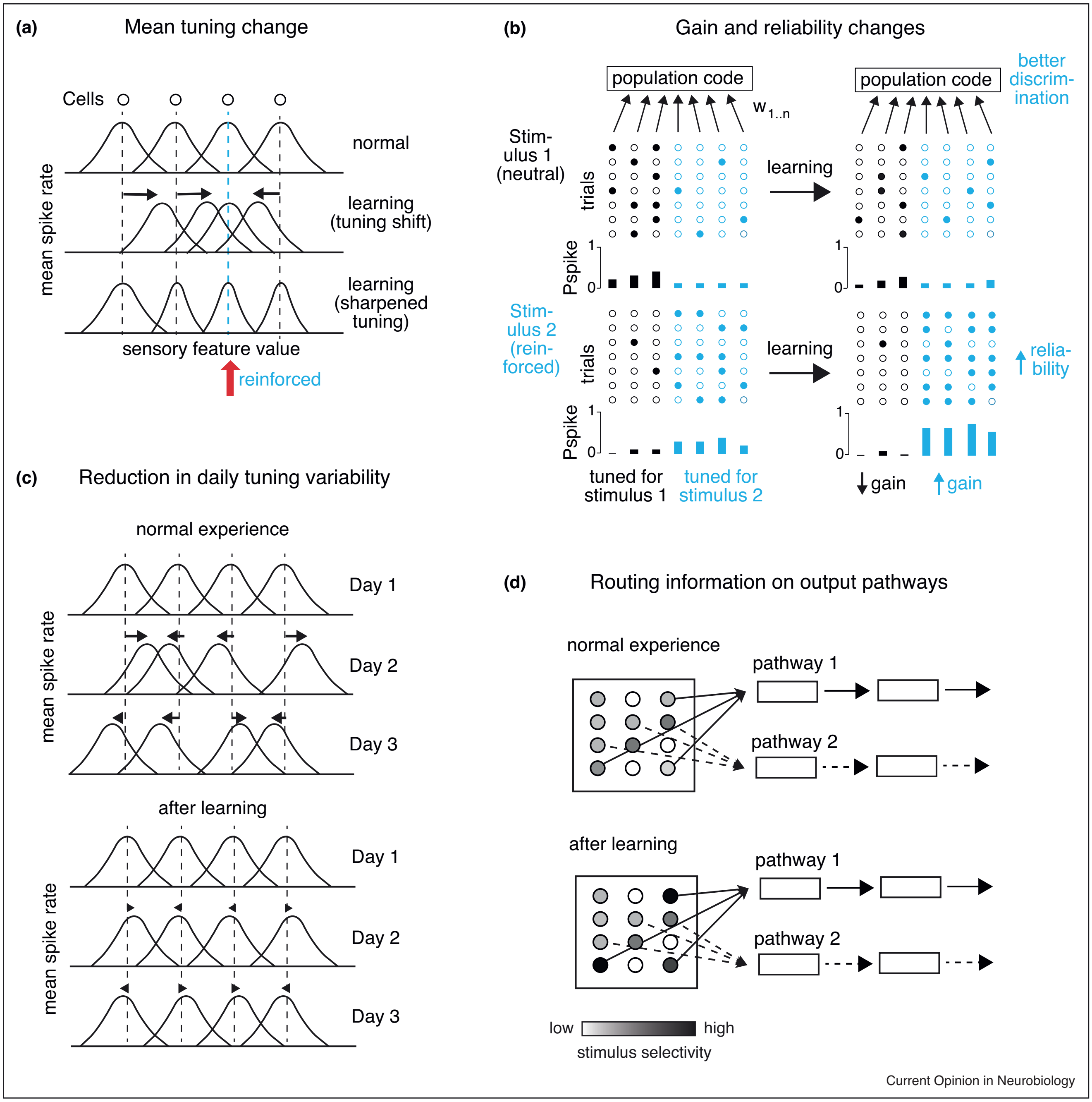
In classical map plasticity, neurons adjust their sensory tuning to represent common or behaviorally relevant (i.e. reinforced) sensory features. This is confirmed by population imaging. In mouse V1, filtering out all but one visual orientation in juveniles increases the proportion of neurons tuned to that orientation [7]. In adults, monocular deprivation causes 60% of active neurons to shift ocular dominance toward the open eye, though a minority shift paradoxically to favor the closed eye [8••]. In S1, a large majority of neurons similarly shift whisker tuning away from deprived whiskers and toward a spared whisker [9]. Hebbian plasticity mechanisms are thought to underlie many of these changes. The ability of Hebbian plasticity to imprint information in sensory cortex has been shown decisively in V1, where optogenetic coactivation of L2/3 pyramidal (PYR) cells induces Hebbian-like ensembles that are spontaneously active, exhibit pattern completion, and are spatially mixed with visual-related ensembles [10•].

Cortical plasticity is also induced by training on sensory tasks. Sensory training often alters sensory tuning in neurons representing relevant sensory features [1,11–14,15••]. These include shifts or expansions in tuning toward trained features [1,14,16] or sharpened selectivity that improves population-level discrimination [11,12] (Figure 1a). Training can also shape more complex integrative tuning features, such as tuning for visual contours [13,17]. In some cases, tuning changes are small or absent in primary cortex, but observable in higher sensory or sensorimotor areas (e.g. [12,18]), or occur in primary cortex only transiently [16]. Thus, tuning changes in primary cortex are one mechanism, but not the only mechanism, for perceptual learning.

Principles of population coding in sensory cortex

Sensation occurs on single trials, despite noisy spike data. Population codes are robust on single trials because they utilize statistical patterns of activity across large numbers of neurons. Both population spike recording and population imaging have been used to characterize population coding in sensory cortex. Here we focus on population imaging, which typically samples more neurons, often with cell type specificity, and has revealed several key features of population coding in sensory cortex.

Figure 1



Four ways to adjust a population code in sensory cortex. **(a)** Systematic changes in sensory tuning by single neurons. Each curve is tuning of a different neuron, along a sensory feature axis. Neurons shift or sharpen their tuning to better represent common or reinforced stimulus features. **(b)** Changes in sensory gain and response reliability. Each circle represents activity of a neuron on a given trial (filled: spiking, open: not spiking). Subpopulations of neurons are tuned for stimulus 1 or 2. Before training, response gain and reliability are relatively low, leading to poor discrimination on the population level. During learning, gain and reliability to the reinforced stimulus increase, increasing reliability of the population code. **(c)** Reduction in day-to-day tuning variability. Under normal sensory conditions, sensory tuning of individual neurons changes from day to day. During learning, this variability decreases, so that population decoding becomes more stable and accurate. **(d)** Routing of information on output pathways from primary sensory cortex. Intermixed subpopulations of neurons project to different output pathways. With learning, one subpopulation increases stimulus selectivity or responsiveness, thus routing information preferentially down one pathway.